

Biogeography of the Freshwater Peracarida (Crustacea) from Barrington Tops, NSW

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Distributions of certain groups of freshwater Peracarida (Crustacea: Isopoda; Amphipoda) in south-eastern Australia are known to favour high altitudes with associated cooler temperatures. Two species of crangonyctoid amphipod (*Austrocrangonyx barringtonensis* and *A. hynesi*) and two phreatoicid isopod species (*Crenoicus harrisoni* and *Crenoicus* n. sp.) have previously been documented from the Barrington Tops. During this study, six peracarid taxa were located including two new generic records for this area. These taxa showed interspecific variation in habitat and altitudinal preference on the Barrington Tops Plateau (~1585 m). The most influential environmental determinants of distribution for certain taxa were pH, flow rate and altitude according to canonical correspondence analysis (CCA). As a result, an altitudinally tiered distribution pattern could be seen on the plateau with *Pseudomoera* n. sp., the most tolerant taxon, occupying the widest range of altitudes and habitats. A broader investigation of peracarid distribution on the adjacent Nundle-Walcha Plateau to the north of Barrington and at Coolah Tops to the west, indicated the effects of past climate changes and remaining areas of refugia. Various levels of geographic speciation were identified relating to differences in adaptability and vagility between the amphipods and phreatoicid isopods.

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INTRODUCTION

The Peracarida are of ancient lineage and are regarded as 'living fossils', with extant freshwater forms having undergone relatively little change from their ancestral marine relatives (Nicholls 1929). Two groups of present interest, the phreatoicid isopods and the crangonyctoid amphipods, have Gondwanan distributions and occur mainly in the cooler southern parts of Australia (Williams 1981, 1983). As might be expected from such distributions, many of the more northerly localities are at higher altitudes, especially among the amphipods. The Barrington Tops area (up to 1585 m asl) are known to have two amphipods, *Austrocrangonyx barringtonensis* and *A. hynesi* (Williams and Barnard 1988), and an isopod, *Crenoicus harrisoni* (Nicholls 1943). In addition, a species related to the recently described *C. buntiae* from the Boyd Plateau 300 km to the south-west (Wilson and Ho 1996) is known to occur at Barrington Tops (G. Wilson, pers. comm.).

The aims of this work are: (a) to investigate the occurrences of Peracarida in the Barrington Tops and adjacent environs, map their distribution and assess their current status of abundance, and (b) to outline the habitat and altitude preferences of the taxa concerned. In addition, given the preference of many amphipods for cold temperatures

and their use in environmental monitoring (Lake et al. 1979; Kangas and Geddes 1984), the mapping of present distributions may provide a basis for measuring the effects of future climatic change.

STUDY AREA

Barrington Tops Plateau ($32^{\circ}00'E$, $151^{\circ}30'S$) is located 150 km north-west of the coastal city of Newcastle (Fig. 1). It is a remnant isolated paleoplain at 1000-1585 m asl and is bordered by steep escarpments (Pain 1983). The plateau surface is undulating with several, poorly drained valleys leading into deeply dissected ravines with steep stream gradients of the Manning River to the north and east and of the Hunter River to the south and west. Connected by a broad ridge, Gloucester Tops lies at 1313 m asl, while the disconnected Mount Royal at 1400 m asl represents the southern limit of higher altitudes. The northern high altitude limit is delineated by lower relief located at the Pigna Barney River which separates the Barrington Tops Plateau from a southern extension of the New England Plateau in the Nundle-Walcha district. This plateau has an altitudinal range of 1000 to 1400 m which cuts off steeply to the east and south with a gradual descent to the north, and is dissected by rivers and gorges. Drainage is into three major catchments; the Manning and Macleay Rivers to the east and south and the Namoi River to the west which constitutes part of the Murray-Darling system. A smaller isolated plateau (Coolah Tops $31^{\circ}45'E$, $151^{\circ}05'S$) lies 140 km to the west with an altitudinal range of 1000-1200 m and stream systems running into the Namoi and Macquarie Rivers (refer to Fig. 1).

The Barrington Tops area has a cool-temperate climate with frequent frosts and occasional snow falls in winter. Rainfall is evenly distributed throughout the year and a strong precipitation gradient from 2000 mm p.a. occurs on the eastern side at Gloucester Tops to 1000 mm p.a. on the western side of Barrington Tops (Dodson 1987). The mean temperature range in July at 1300 m is -2.3 to $8.8^{\circ}C$ with the January range at $9.1-22.8^{\circ}C$



Figure 1. Location of the study area.

(Dodson 1987). To the south, Mt Royal experiences an average rainfall of 1100 mm p.a., a mild to cool-temperate climate and temperature ranges of 15-30°C in summer and 3-15°C in winter (Kinhill 1992). Barrington Tops supports a diverse range of vegetation from sub-alpine grasslands, open montane eucalypt forests, Sphagnum bogs and sedgelands on the plateau surface, to cool temperate rainforest and sclerophyll on the lower slopes. The plateau is used recreationally in National Park and State Forest areas with selective logging taking place in the latter. Private land in the northern area has been cleared for pastoral use.

The majority of the Nundle-Walcha district is used for grazing with pockets of State Forest areas and pine plantations. Many swamps occur on private land, some of which have been drained to increase stock carrying capacity.

METHODS

A systematic search of the Barrington Tops and adjacent highland regions was conducted during the warmer seasons of spring and summer from February 1995 to March 1996. Sites were selected so as to include all major catchments, a range of altitudes and habitats, and any orogenic/ecological barriers within the areas which may affect population distributions. A total of 64 sites (alt. range of ~ 392-1500 m) were sampled in the Barrington Tops - Mount Royal area (Fig. 2). These sites were analysed to determine overall habitat preferences and distributional tendencies. A further 38 sites (alt. range of ~ 920-1345 m) from the Walcha-Nundle and Coolah Tops areas were investigated less intensively to provide information on distribution range and diversification of the peracarid taxa.

Two different sampling techniques were used to collect amphipods and isopods. Sampling for amphipods employed a hand-held net with a mesh size of 1 mm positioned on the creek bed facing the current. A modification of 'kick' sampling (Frost et al. 1970; Chessman 1995) was used whereby rocks and underlying substrate were disturbed by hand causing the animals to be washed into the net. Contents were emptied onto a large white tray from which all specimens could be field picked. For isopods, a kitchen sieve with a mesh size of 1 mm was used for sampling along creek edges and in swamp areas. A 'sieving and winnowing' technique was used (G. Wilson, pers. comm.) that produced a clean sample from which to pick specimens. Sites yielding peracarid specimens were called 'positive' sites, while 'negative' sites gave no peracarideans. The collections (omitting actual sorting) were timed to assess abundance at each site. All specimens were transferred to vials containing 100% methylated spirits and stored for later identification and abundance counts. Ranked abundance was determined by dividing the number of specimens of each taxa in the sample by the time taken for the sample collection. These results were assigned to an abundance rank on a four point scale (see Table 2 and for details refer to Adlem 1996).

At the Barrington sampling sites, temperature, pH, conductivity, dissolved oxygen and turbidity were measured using a calibrated Horiba water testing unit and momentary flow rate using a hydrometer. Degrees of exposure and turbulence were visually assessed and designated to a numerical scale (see Table 4). Overlying and underlying substrate were defined by diameter ranges, and vegetation (both aquatic and terrestrial) was identified and recorded at least to the genus level. Each immediate collection point was noted as a 'midstream', 'edge', 'riffle', 'pool' or 'roots' sample. Altitude and stream order were taken directly from 1:25 000 topographical maps as was distance from tributary sources using a curvimeter.

Barrington site data were analysed using the FORTRAN program CANOCO for a direct correspondence analysis to indicate species/environment relationships. Canonical Correspondence Analysis (CCA) is a one-step analysis incorporating eigenvector ordination and multivariate direct gradient analysis (Ter Braak 1986). CANOCO (version 2.1) was

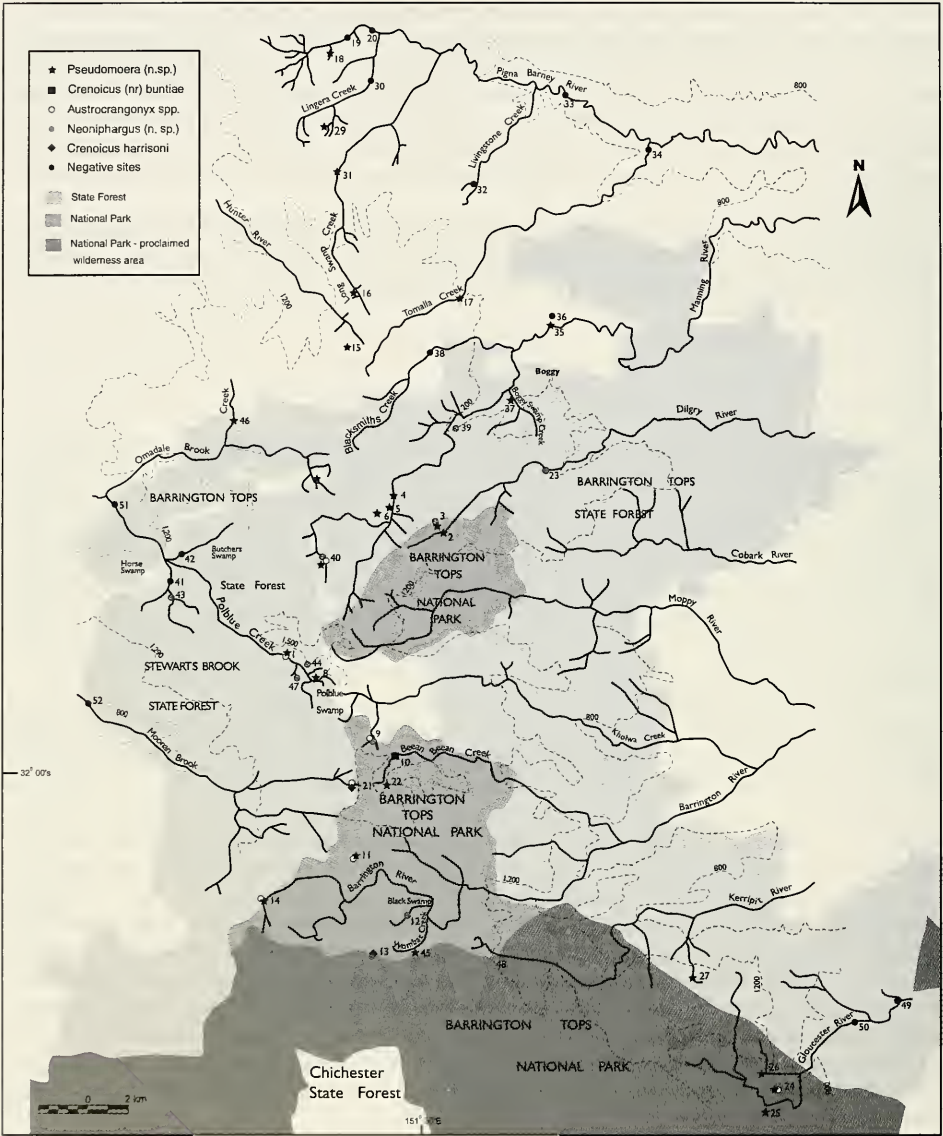


Figure 2. Location of study area sites with respective Peracarida collected.

run in a weighted centroid linear mode to combine physical data along which species data was distributed in accordance with influential environmental variables. Data such as exposure, temperature and dissolved oxygen were omitted from the analysis because of high variability owing to diurnal change. The resulting weighted mean scores were plotted on ordination axes to construct bi-plots. From these plots habitat preferences incorporating quantitative, ranked and qualitative data could be assessed and interpreted according to the positioning of corresponding coordinates.

RESULTS

Peracarida were collected from all major catchments. Four aquatic genera were found within the Barrington Tops study area, three of which were also present in the external exploratory areas in the Nundle-Walcha and Coolah districts. Terrestrial specimens were also found within collections (Table 1). Specimens with features approaching *Crenoicus buntiae* were collected from several sites and are referred to as *C. n. sp.* Both *Austrocrangonyx hynesi* and *A. barringtonensis* were present on the Barrington Tops, although a significant feature intergradation between the two species occurred with *A. barringtonensis* being predominantly identified (see Adlem 1996).

Table 1. Taxonomic segregation of the peracarid fauna collected from the Barrington Tops Plateau.

ORDER	FAMILY	GENUS	SPECIES	Aquatic/Terrestrial A/T
Amphipoda	Paramelitidae	<i>Austrocrangonyx</i>	<i>A. barringtonensis</i>	A
			<i>A. hynesi</i>	A
	Eusiridae	<i>Pseudomoera</i>	n.sp	A
	Neoniphargidae	<i>Neoniphargus</i>	n.sp	A
	Talitridae	<i>Arcitalitris</i>	<i>A. sylvaticus</i>	T
Isopoda	Phreatoicidae	<i>Crenoicus</i>	<i>C. harrisoni</i> n. sp.	A A
	Oniscidae	?	?	T
Total	6	6	9	

Neoniphargus sp. and *Pseudomoera* sp. in the Barrington region are new generic records and are of new species (J. Bradbury, pers. comm.). Sites sampled in the Nundle-Walcha district included further new species of *Pseudomoera* and *Austrocrangonyx*, and undescribed species of *Crenoicus*. *Crenoicus* spp. were the most frequent taxa encountered on the Nundle-Walcha plateau, being collected from 72% of positive sites. However, abundance ranks were generally low, particularly in swamp areas (see Appendix 2 in Adlem 1996). *Pseudomoera* sp. b was collected from a single site in this district which at present is the most northern locality for this genus. *Crenoicus* sp. was also found inland at Coolah Tops from a single site but no amphipods were present in this area.

Of the 64 sites sampled in the study area, 44 yielded collections of Peracarida. The sites in the Mount Royal State Forest yielded no specimens. *Pseudomoera* proved to be the most abundant (Table 2) and widespread taxon on the Barrington Tops plateau, being located at sites both within State Forest and National Park boundaries and externally on private land to the north. *Austrocrangonyx*, *Crenoicus* and *Neoniphargus* were all located at sites within these boundaries with *Neoniphargus* n. sp. and *C. harrisoni* (site13) co-occurring at the single locality in the upper reaches of the Manning River. *Pseudomoera* occurred at lower altitudes and consequently in higher order streams than the other taxa which were all found at distances <3 km from tributary sources at altitudes above 1000 m (see Adlem 1996).

A broader distribution of *Pseudomoera* was also indicated by its occurrence within a wider altitudinal range (Table 2). The diversity of freshwater peracarid fauna increases with increasing altitude with the richest zone being 1400-1500 m. Therefore, 50% of the taxa found lie between 1200-1400 m. *Austrocrangonyx* is also relatively widespread and abundant (Table 2), but only occurred above 1100 m.

TABLE 2. Number and percentage of positive sites (n = 44) occupied by peracarid taxa in the study area with abundance expressed as mean rank values. Mean abundance values ranked as 1 = lowest abundance; 4 = highest abundance. NA = not applicable (single sites).

*Refer to Adlem, 1996.

	No. sites occupied / %	No. species exclusive sites / %	Mean abundance rank value.*
<i>Pseudomoera</i> sp.	34 / 77.3%	24 / 54.5%	2.2
<i>A. barringtonensis</i>	11 / 25.0%	1 / 2.3%	1.4
<i>C. n. sp.</i>	9 / 20.5%	8 / 18.2%	1.2
<i>A. hynesi</i>	3 / 6.8%	0	1.0
<i>Neoniphargus</i> n. sp.	1 / 2.3%	0	NA
<i>C. harrisoni</i>	1 / 2.3%	0	NA

The two bi-plots depicting species-environment relationships from the CANOCO analysis (Fig. 3) were produced simultaneously, therefore the respective plotted points represent integral ordination results.

TABLE 3. Relationships between environmental vectors and ordination axes.

Vector	Axis	Weighted CCA Correlation Value
Altitude	1	(-) 0.5610
	2	0.5129
Mean Flow Rate	1	0.6091
	2	0.6212
Turbidity	1	(-) 0.5715
	2	(-) 0.0004
Conductivity	1	0.2902
	2	(-) 0.1297
pH	1	0.7273
	2	(-) 0.4632
Turbulence	1	0.3200
	2	0.1741

Fig. 3a shows the plotted coordinates obtained for taxa and environmental vectors which are represented by lines. The increasing length of these lines indicates increasing magnitude of the respective vector, while position corresponds to the direction in which the vector is undergoing its greatest variability or change. The positioning among vectors relates to the degree of correlation between them. Therefore, vectors that oppose one another in the bi-plot have a negative correlation in regard to their respective increasing magnitudes. Hence, greater turbidities were negatively correlated with higher flow rates or more turbulent conditions, and less acid waters were negatively correlated with the higher altitudes on the plateau. Table 3 shows that the vectors with the longest lines (altitude, pH and mean flow rate) have higher correlation values with regard to the axes and are therefore the most influential factors towards the plotted positions of taxa and sites.

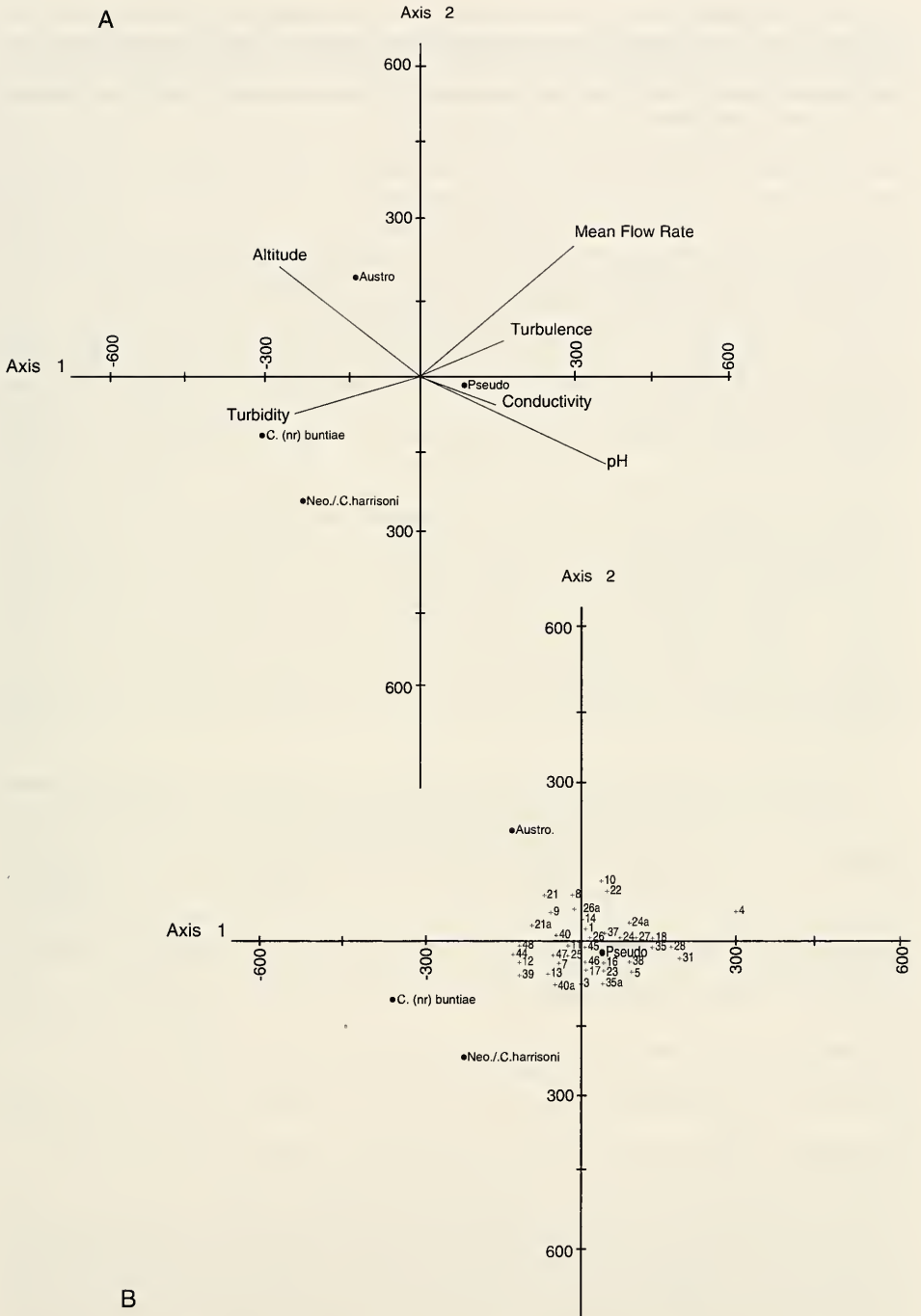


Figure 3. Canonical correspondence analysis bi-plots showing the degree of correlation of species abundance with environmental vectors (A) and corresponding sites (B).

Fig. 3b depicts plots of taxa in relation to corresponding positive sites where the respective taxa were located in greatest abundance. Altogether, Fig. 3 gives an indication of taxa plotting nearest to the vectors and sites to which they are most highly correlated, therefore the area of the bi-plot can be seen to represent a distance matrix originating from the mid-point, zero.

Because all data are weighted linearly, the plots of *Austrocrangonyx* positive sites between altitude and mean flow rate show a correlation with higher altitudes, faster flow rates and greater turbulence. Opposing vectors to these sites are pH and conductivity, indicating lower values of these parameters (i.e. more acid, fresher waters) influencing the location of *Austrocrangonyx* sites. The most strongly corresponding site plot was sampled from roots of *Sphagnum* (site 21) with sites in shallow, stony riffle zones (21, 26a, 14 and 8) also distinctly conforming to abundant collections of this taxon.

As shown in Fig. 3a, *Pseudomoera* plotting near the origin of the axes suggests all vectors as corresponding somewhat universally with this taxon, as the locus at the origin implies an equal influence of each vector, and no one vector is dominating the plot. Although plotting closely to conductivity and turbulence, these parameters did not correlate highly with either axis (Table 3), and therefore cannot be seen as strong influential factors in affecting *Pseudomoera* occurrences. Therefore, this central positioning reflects the ubiquitous range of *Pseudomoera* located with a greater variability of vectors implying a tolerance to a wide range of environmental conditions (excepting turbidity) in comparison with the other taxa as shown by raw data ranges shown in Table 4. Consequently, *Pseudomoera* was also found in a wide range of habitats which is supported by the majority of sites clustered around this taxon. These habitats ranged from deep, standing water within root systems of *Myriophyllum aquaticum* in muddy substrate (site 3), to fast-flowing, shallow riffle zones (2a and 38). However, the most abundant collection of *Pseudomoera* was at site 18 sampled from root systems of *Nasturtium*. Mossy rocks and liverworts in riffle zones of rainforest areas (24, 26, 27 and 45) also produced large numbers of this amphipod.

TABLE 4. Raw data ranges of the environmental parameters analysed within which taxa were found in the study area. Turbulence values ranked as 1 = lowest degree of turbulence; 4 = highest degree. NR = not recorded. *Refer to Adlem, 1996.

Parameter → Taxa ↓	Altitude (m)	Turbidity (NTU)	Turbulence*	Conductivity (μ S/cm)	pH	Mean Flow Rate (cm/sec)
<i>Austrocrangonyx</i>	1168-1490	0.0-0.6	1-4	20-43	5.5-6.4	11.3-42.1
<i>Pseudomoera</i>	865-1500	0.0-2.0	1-4	25-352	5.5-7.7	0.0-80.3
<i>Neoniphargus</i>	1400	0.0	3	17	6.0	NR
<i>C. n. sp</i>	1260-1495	0.0-6.3	3-4	17-45	4.8-6.7	0.0-21.2
<i>C. harrisoni</i>	1440	0.0	3	17	6.0	NR

The position of both *Crenoicus harrisoni* and *Neoniphargus* n. sp. coordinates plotted further away from vectors and sites. This is due to the rare occurrence of these species from a single site causing the plot to fall outside of the bounds of strong correlation and correspondence owing to a weaker data set. At site 13, *Crenoicus harrisoni* was observed to favour patches of gravel substrate within mud supporting *Ranunculus* and *Montia*, while *Neoniphargus* n. sp. was more prevalent among the root systems of these macrophytes.

The plot of *Crenoicus* n. sp. at the end of the turbidity vector indicated the strongest correlation on the bi-plot. Strongly opposing vectors of mean flow rate and turbulence suggest a tendency of this taxa to prefer slow flowing or standing waters with greater turbidities (Table 4). This species of *Crenoicus* was collected from roots of *Myriophyllum* (sites 12 and 48), *Ranunculus* (site 39) and *Sphagnum* (sites 21a and 44).

DISCUSSION

This study has shown a greater diversity of freshwater Peracarida than has previously been recognised from the Barrington Tops Plateau, with at least six species located in the area. The occurrences of *Austrocrangonyx* spp. at higher altitudes above 1100 m in the uppermost headwaters demonstrates that *Austrocrangonyx* is a cold water, rheocolous taxon, favouring fast-flowing, shallow riffle zones, also noted in the Nundle-Walcha district during this study and by Boulton et al. (1995). The distribution of *Austrocrangonyx* was related to waters with lower pH values (Fig. 3a) which, at higher altitudes, are primarily influenced by the presence of the humic, peat-based swamps situated on the poorly drained plateau surface.

Pseudomoera is the most commonly occurring and widespread taxon on the plateau, also occurring in the northern pastoral areas in creeks at lower altitudes with higher conductivities, greater turbidities, and higher pH levels associated with the absence of swampland and presence of exposed basalt surfaces. The high degree of abundance and occurrence of this amphipod would also be influenced by its ability to breed all year round as opposed to seasonal breeding in the other species (see Adlem 1996).

The distribution of *Crenoicus* spp. on the Barrington Tops Plateau is strongly determined by the extent of *Sphagnum* areas and macrophyte establishment as populations were seen to favour these environs. Amphipods were also observed in the root systems of aquatic macrophytes common to the area (*Myriophyllum* and *Ranunculus*) although not as abundantly as the phreatoicid isopods. *Crenoicus* sp. (nr.) *buntiae* preferred deeper, more turbid, slower flowing creeks with localised depositional areas of suitable substrate for the establishment of *Myriophyllum aquaticum*. *Myriophyllum* is known to occur prolifically in waters containing a high nitrogen content (Sainty and Jacobs 1981) which would become more available to the plants under acidic conditions (Salisbury and Ross 1985). Therefore, the acidic waters in the swamp vicinities contribute to a larger extent of available habitat for *Crenoicus* spp., from the fibrous peat and root systems of *Sphagnum* to basal sections of *Myriophyllum* in associated creeks draining out of and into swamp areas. Consequently, the most abundant occurrences of *Crenoicus* spp. were concentrated at sites located on the southerly plateau surface where swamps and alpine sedgeland communities dominate.

Crenoicus spp. are widespread in the highlands of mid-eastern Australia (G. Wilson, pers. comm.), therefore their extensive occurrence within both the study area and exploratory areas is not surprising and new species on the adjacent plateau reflects strong divergence.

The distributional ranges of certain taxa from the Barrington plateau proved to be much wider than formerly recorded. The discovery of a new species of *Austrocrangonyx* (J. Bradbury, pers. comm.) to the north on the adjacent Nundle-Walcha plateau indicates that this genus has a widespread, discontinuous distribution and is therefore not endemic to the Barrington area. *Austrocrangonyx* has also been found by one of us (BVT) near Ebor above 1200 m, which may well be the northernmost limit for this taxon. Freshwater amphipods have not been recorded from the Dorrigo State Forest area north of Ebor despite suitable altitudes (ca. 1380 m) (Chessman et al. 1994). Based on collection data for the Barrington-New England area however, the Nundle-Walcha plateau appears to be the northern limit of distribution for *Pseudomoera*.

The catchment divides (which in these plateau areas are low) are unlikely to be

barriers to dispersal for peracarids. The occurrence of *Austrocrangonyx*, *Pseudomoera* and *Crenoicus* spp. (e.g. *Crenoicus* n. sp.) in the Hunter and Manning catchments and also to a lesser degree in the Namoi which is part of the inland Murray-Darling system indicate a current widespread distribution. However, small scale isolation effects, particularly on the Nundle-Walcha plateau where agricultural and forestry operations are more prevalent, may contribute to habitat fragmentation and therefore loss of habitat area for peracarids.

The fossorial *Neoniphargus* is likely to be a rare, relict species, and therefore an indicator of the Barrington area offering high altitude refugia for such forms. The cold water relict amphipod fauna mentioned by Williams and Barnard (1988) and Barnard and Barnard (1983) are included in the crangonyctid group of which both *Austrocrangonyx* and *Neoniphargus* are representatives.

The occurrence of *Crenoicus* and absence of amphipods at Coolah Tops is significant. The only permanent waters are located at the head of the Talbragar River where *Crenoicus* was found. Though altitudes (and therefore temperatures) are marginal for amphipods (based on data from Barrington Tops) no amphipods, including the more tolerant *Pseudomoera*, were found. During a past arid phase, as for example ca. 18,000 years ago (De Deckker 1986), all streams in the Coolah Tops region would be intermittent at best and hence unsuitable for amphipods. Therefore, if amphipods ever existed at Coolah Tops, a past climate change would have caused their extinction there. However, phreatoicid isopods have the ability to sustain themselves at the sediment/groundwater interface, and could have survived dry periods. Lower altitudes, relatively dry conditions and temporary habitat also explains the lack of amphipods from the Mount Royal State Forest area. The upper reaches of tributaries where amphipods would be expected to be found were drought affected in this area.

The distribution of the aquatic Peracarida observed in this study indicates that both Barrington Tops and the adjacent plateau in the Nundle-Walcha region maintain suitable refugia and habitat area for these crustaceans. The amphipod relict fauna appears to have a predisposition to colder environments and permanent waters which is corroborated by their absence from Coolah Tops. Colder habitat and refuge areas on both plateaus are indicated by the widespread presence of *Austrocrangonyx*. The high altitude, cold water distribution of the amphipods may suggest that these animals could be monitors of possible future climate change, with *Pseudomoera* at the lower altitudes being a primary marker.

The distribution pattern of the amphipods relates to colder temperatures in tributary headwaters and higher altitudes, whereas the phreatoicid isopods appear to have an overall wider habitat distribution and stronger divergence levels. The different distribution patterns between the amphipods and the phreatoicid isopods is related to their differing levels of vagility and adaptations to their respective environments.

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